

## Tertiary Sciuridae (Mammalia: Rodentia) from Bavaria

CRAIG C. BLACK, Pittsburgh\*)

With plates 4—6

### Summary

Material pertaining to the rodent family Sciuridae is described from Tertiary localities in Bavaria. One new species of flying squirrel is named. *Sciurus schlosseri* is identified as a pseudosciurid and *Paracitellus eminens* as a paramyid. The taxonomic status of *S. chalaniati* is discussed and certain specimens referred to that species are identified as glirid.

### Zusammenfassung

Material der Nagerfamilie Sciuridae von tertiären Fundstellen in Bayern wird beschrieben. Eine neue Art Flugeichhörnchen wird benannt. *Sciurus schlosseri* wird als Pseudosciuride und *Paracitellus eminens* als Paramyide erkannt. Der taxonomische Status von *Sciurus chalaniati* wird diskutiert; einige bisher zu dieser Art gestellte Stücke gehören zu den Gliriden.

### Introduction

The first species of the family Sciuridae to be recognized in Tertiary deposits was named by H. VON MEYER in 1846 on material from the Aquitanian Weissenau fauna of the Mainz basin. Specimens of this species, *Spermophilus speciosus*, were neither figured nor described and in 1884 SCHLOSSER synonymized it with *Sciurus feignouxii* POMEL from the Aquitanian St. Gérard fauna. Although *Sciurus feignouxii* was also neither figured nor described when originally named by POMEL (1853), this species was adequately characterized by FILHOL (1879) and has been referred to consistently in the literature since that date. Under the latest rules of the International Code of Zoological Nomenclature (1961), *S. feignouxii* should certainly be taken as the valid name since (1) *S. speciosus* does not appear in the literature after 1884, (2) *S. feignouxii* has been well documented, and (3) it is the name which has been in use since 1884.

In 1848 VON MEYER named another species of sciurid, *Sciurus bredai*, from the late Vindobonian Oeningen fauna of southern Germany, but again the

\*) Dr. CRAIG C. BLACK, Carnegie Museum, 4400 Forbes Avenue, Pittsburgh, Pa. 15213 USA.

material was neither figured nor described. DEPÉRET (1887) described *Sciurus spermophilinus* from La-Grive-St.-Alban. SCHLOSSER (1884, p. 70) gave measurements and a brief description of the type specimen of *S. bredai*. This description was taken from a sketch of VON MEYER's specimen deposited in Munich. Later, however, (SCHLOSSER 1890) he synonymized *S. bredai* and *S. gervaisianus* with *S. spermophilinus*. Additional material was referred to *Sciurus spermophilinus* by MAJOR (1893) and then in 1899 MAJOR presented a figure and further description of the specimen on which VON MEYER had based *Sciurus bredai*. This specimen is now in the collections of the British Museum (Natural History). MAJOR (1899) pointed out that *S. bredai* and *S. spermophilinus* were synonymous but that SCHLOSSER's (1884) description of the *S. bredai* type gave *S. bredai* priority over *S. spermophilinus*, which was not described until 1887. STROMER (1940) followed MAJOR in recognizing *S. bredai* as the valid name. Under the latest rules of the International Code of Zoological Nomenclature (1961), *S. bredai* is certainly the valid name. Since VON MEYER's early contributions, a number of workers (SCHLOSSER 1884; DEHM 1937, 1950; STROMER 1928, 1940; FREUDENBERG 1941; and SCHALK 1957) have described additional sciurid material from localities in Bavaria; and, in recent years, several new Vindobonian and one possibly early Pontian faunule containing sciurid remains have been recovered from the Molasse of Bavaria by Professor DEHM and his assistants at Munich.

While working on a general review of the European Tertiary Sciuridae, I spent several weeks studying these collections in Munich and, through the kindness of Prof. DEHM, this new material was turned over to me for study. The purpose of the present report is two-fold; first, to describe the new materials from the Vindobonian and (?) early Pontian; and second, to clarify the systematic position of several species in the Munich collections assigned by earlier workers to the Sciuridae. Only those species previously described whose assignment to the Sciuridae is either incorrect or open to some doubt will be considered here; other species which are unquestionably sciurid will be dealt with in the general review of European sciurids now in preparation. All but one of the specimens discussed below are from the Tertiary of southern Germany, the exception being *Sciurus schlosseri* which is from the Phosphorites de Quercy but was described by FREUDENBERG (1941) in his review of the rodents from Gaimersheim.

The new material consists, in large part, of isolated teeth obtained through the use of washing techniques. In most cases these specimens can be referred to species previously described from other Vindobonian localities in Europe. However, at two localities the sciurid elements of the faunules are quite different from any previously known. One of these faunules, Giggerhausen, is latest Vindobonian in age, while the other, Markt, is considered by DEHM (1955) and FAHLBUSCH (1964) to be somewhat younger in age, possibly early Pontian.

I would like to express my thanks to Prof. DEHM and Drs. OETTINGEN and FAHLBUSCH for their many kindnesses and assistance to me during my stay in Munich and for allowing me to describe this material. I would also like to thank

Prof. H. TOBIEN of Darmstadt for allowing me to include here some observations on sciurid material from Wölfersheim in the collections at Darmstadt. I also thank Dr. MARY DAWSON who has read the manuscript and offered many helpful suggestions. The illustrations were made by Mr. OTTO GARRAUX of Basel and the stereo photographs by Monsieur R. SIMON of Paris. This study was made possible by a grant from the National Science Foundation, GB-1266. All specimens discussed in this report are in the collections of the Institut für Paläontologie und historische Geologie in Munich.

### Vindobonian material

**Burgau:** Only one specimen of a sciurid consisting of associated P<sup>4</sup>—M<sup>3</sup> is represented in this fauna. Although somewhat larger than the Oeningen and La-Grive material of *Sciurus bredai* this specimen certainly belongs to this group and is best considered as *Sciurus* aff. *S. bredai*.

**Eitensheim:** One tooth of *Sciurus* aff. *S. bredai*.

**Hesselohe:** Four teeth, all of *Heteroxerus* aff. *H. grivensis*.

**Langenmoosen:** The sample from this locality numbers nearly one hundred teeth and at least three species of Sciuridae are represented. *Sciurus* aff. *S. bredai* and *Heteroxerus* aff. *H. grivensis* are the most common but there are also several teeth of a species of *Sciuropterus* that is somewhat smaller than *Sciuropterus albanensis* and quite probably represents a new species. However, the material is insufficient to warrant description at this time.

**Rembach:** Three teeth indicate the presence of *Sciuropterus* and *Sciurus* aff. *S. bredai*.

**Niederaichbach:** Six teeth of *Sciurus* aff. *S. bredai*.

**Oggenhof:** Similar to Langenmoosen in sciurid representation with *Sciurus* aff. *S. bredai* and *Heteroxerus* aff. *H. grivensis* most common but with species of *Sciurus* and *Sciuropterus* also present.

**Pöttmes:** Two teeth, one of *Heteroxerus* and one of *Sciurus* aff. *S. bredai*.

**Münchsmünster:** One tooth of *Sciurus* aff. *S. bredai*.

**Rosshaupten:** Four isolated teeth representing *Sciurus* aff. *S. bredai* and *Heteroxerus* aff. *H. grivensis* and one mandible with P<sub>4</sub>—M<sub>3</sub> of *Sciuropterus* cf. *S. albanensis*. There are a few minor differences between this specimen and the type, but they are probably not sufficient to warrant specific separation for the Bavarian population. The enamel of the talonid basins is not as rugose, the mesoconid is not as large, and the buccal arm of the anterior cingulum is not as well developed as in the La-Grive population.

S a n d e l z h a u s e n: Another large sample of isolated teeth similar to the Langenmoosen sample in sciurid species present, with *Sciurus* aff. *S. bredai* and *Heteroxerus* aff. *H. grivensis* most common and *Sciuropterus* sp. and *Sciurus* sp. also present.

G i g g e n h a u s e n: There are five isolated teeth and one fragment of mandible with P<sub>4</sub>—M<sub>1</sub> from this locality: three of the teeth are those of a small species of *Sciuropterus*; the others represent an extremely small and unusual sciurid of indeterminate affinities.

*Sciuropterus* cf. *S. gaudryi*

Plate 4, fig. A—B, Plate 5, fig. C

M a t e r i a l: Munich 1952 XIV 20, RP<sup>1</sup>; 1952 XIV 293, RM<sup>1 or 2</sup>; 1952 XIV 295, RM<sup>3</sup>.

D e s c r i p t i o n: The three specimens here referred to *Sciuropterus* cf. *S. gaudryi* are all of the proper size to belong to this species. No upper cheek teeth were known of *S. gaudryi* at the time of its description (GAILLARD, 1899, p. 66) and none have been reported to date. *S. gaudryi* is by far the smallest species of the genus (length P<sub>4</sub>—M<sub>3</sub>, 5.7, as compared with 13.8—14.5 for *S. albanensis*) and on the basis of size these teeth are referred to *S. gaudryi*. They all have high, sharp protocones bounded anteriorly and posteriorly by deep lingual indentations, conules that are large and sharp on P<sup>1</sup> and M<sup>3</sup> but not distinct on M<sup>1 or 2</sup>, and accessory ridges from the high, thin lophs on P<sup>1</sup> and M<sup>1 or 2</sup>. All these characters are typical of other species of *Sciuropterus* and leave little doubt but that these teeth pertain to that genus.

Measurements in mm.

	a—p	tr.
P <sup>1</sup>	1.9	2.1
M <sup>1 or 2</sup>	1.9	2.5
M <sup>3</sup>	2.1	2.3

Sciurid incertae sedis

Plate 4, fig. C—D, Plate 5, Fig. E.

M a t e r i a l: Munich 1952 XIV 21, fragment of left mandible with P<sub>4</sub>—M<sub>1</sub>; 1952 XIV 288, LM<sub>1 or 2</sub>; 1952 XIV 292, RP<sup>1</sup>.

D e s c r i p t i o n: The cheek teeth are very small, approaching in size those of the Recent pigmy squirrels, *Myosciurus* and *Nanosciurus*, but showing no resemblances to pigmy squirrels in their crown patterns. This sciurid is smaller than any previously reported from the Tertiary.

In crown pattern the teeth are simple, particularly the lower cheek teeth. The primary cusps of P<sup>4</sup> are high and sharp with the protocone compressed anteroposteriorly so that in occlusal outline the tooth presents a triangular appearance. The anterior cingulum of P<sup>4</sup> is wide and stretches across the entire

face of the tooth, terminating in a high parastyle buccally. The protoloph and metaloph are complete but quite narrow, with the metaloph lying at a lower level than the protoloph. There are no conules present in the loph. There is a thin ridge across the buccal face of the tooth between the paracone and metacone which bears a small mesostyle. The metaloph forms most of the posterior margin of the tooth with the posterior cingulum reduced to a low, short ledge at the base of the protocone.

The lower premolar and molars are elongate with the talonid basin occupying most of the occlusal surface. Anteriorly the protoconid-metaconid ridge is elevated but there is no anteroconid and only a minute remnant of the trigonid basin is seen in an early stage of wear. The buccal valley is very shallow and there is no distinct ectolophid. No mesoconid or mesostylid is present.

Measurements in mm.			
		a—p	tr.
1952 XIV 292	RP <sup>4</sup>	1.1	1.1
1952 XIV 21	LP <sub>4</sub>	1.2	.9—1.1
	LM <sub>1</sub>	1.2	1.1—1.2
1952 XIV 288	LM <sub>1 or 2</sub>	1.2	1.1—1.2

**Affinities:** It is impossible at present to assign these specimens to any known genus of fossil or Recent sciurid, or even to determine their higher taxonomic affinities beyond stating that they appear to be sciurid. The nearly complete loss of a distinct trigonid basin and anterior cingulum is found today only in the pigmy squirrel, *Microsciurus*, and it is impossible to arrive at any special relationship between a late Vindobonian sciurid from Europe and a Recent South American pigmy squirrel on such scanty evidence.

There are in the collections in Darmstadt several teeth from the late Pliocene Wölfersheim fauna (TOBIEN 1952) that show a strong resemblance to the Giggenhausen material. This suggests that there may have been a lineage of tiny, generalized squirrels in the European late Tertiary that, because of their extremely small size, has escaped previous notice in faunas which have been collected using washing techniques. Further material of this form is badly needed before any statements concerning its relationships can be made.

### ? Pontian material

**Markt 1** (collected by Dr. W.-D. GRIMM, Institut für Allgemeine und Angewandte Geologie und Mineralogie der Universität München): There are two isolated teeth, three lower molars in association, and a fragment of palate with three teeth from this locality. One of the isolated teeth, 1952 X 83 M<sup>1 or 2</sup> (Plate 5, fig. D, Plate 6, fig. C), is that of a small *Sciuropterus* species, similar to *S. gaudryi* but somewhat smaller (meas. a—p 1.7, tr. 1.9); the other, 1952 X 81, is M<sub>1 or 2</sub> and is referable to *Sciurus* cf. *S. bredai*. The three associated lower molars

are described below as a new species of *Sciuropterus* while the palate is described as *Sciurus* sp.

*Sciuropterus grimmi*, n. sp.

Plate 6, fig. D

Type: Munich 1952 X 80, LM<sub>1</sub>—M<sub>3</sub>.

Hypodigm: Type only.

Diagnosis: Largest species of genus; posterolophid higher and thicker than in *S. albanensis* or *S. lappi*; trigonid basin larger than in *S. albanensis* or *S. lappi*; no arm of the anterior cingulum swinging free to the base of the protoconid; metalophid much stronger than in other species of the genus.

Description: The molars increase in size from M<sub>1</sub> to M<sub>3</sub> but M<sub>3</sub> is not as long relative to M<sub>1</sub>—M<sub>2</sub> as it is in *Sciuropterus albanensis* and *S. lappi*. On M<sub>1</sub>—M<sub>2</sub> the trigonid basin is large and bounded by a strong, high, metalophid posteriorly and anteriorly by a lower but heavy anterior cingulum. This area is partially destroyed on M<sub>3</sub> but the metalophid appears to be strong on this tooth. On all three molars the ectolophid is long and low and dominated by a large mesoconid. One of the most striking features of this dentition is the extremely high, heavy posterolophid composed of a swollen entoconid and several other distinct cusps fused into a thick ridge. The mesostylid on M<sub>1</sub>—M<sub>2</sub> is large and projects lingually as a square pillar. There are deep notches between the mesostylid and entoconid and between the hypoconid and posterolophid. The enamel of the talonid basins is not as heavily rugose as in *S. albanensis*.

Affinities: *Sciuropterus grimmi* has its closest affinities with *Sciuropterus lappi*, *Sciuropterus albanensis*, and *Sciuropterus gaudryi* of the Vindobonian. I agree with MEIN (1958) and JAMES (1963) that *Sciuropterus jourdani* (GAILLARD, 1899) and *Sciurus gibberosus* (HOFMANN, 1893) are synonyms of *Sciuropterus albanensis* but also include *Sciurus sansaniensis* (LARTET, 1851) in this synonymy. *Sciuropterus lappi* from Vieux Collonges (MEIN, 1958) is quite similar to *Sciuropterus albanensis* from La Grive but, on the basis of size and a more elongate M<sub>3</sub>, it is probably a valid species. In any case, it is in or close to the ancestry of *Sciuropterus albanensis*. This group of species, *Sciuropterus lappi*, *S. albanensis*, *S. gaudryi*, and *S. grimmi* together with the North American *S. uphami* and *S. matthewsi* (JAMES, 1963) share a number of features which set them apart from the *Pliosciuropterus*-*Petauria* group. *Pliosciuropterus*, described by SULIMSKI (1964) includes *Pliosciuropterus dehnli* and *P. schaubi*, both from Weze, Poland, and probably the species described by DEPÉRET (1890, 1897) as *Sciuropterus pliocaenicus* from Roussillon. Also, probably belonging in the genus *Pliosciuropterus* is an undescribed species in the collections at Darmstadt from the Wölfersheim fauna (TOBIEN, 1952). *Petauria belleri* described by DEHM (1962) and another undescribed Wölfersheim species are much closer to *Pliosciuropterus* than to *Sciuropterus*. This inferred relationship is based upon the presence of a hypolophid or the tendency to develop such a structure in the

former two genera while it is absent in *Sciuropterus*, and the presence of rugosities in the talonid basins of *Sciuropterus* while the talonid basins of *Petauria* and *Pliosciuropterus* are smooth. Also, in the latter two genera the metaconid-mesostylid ridge is strongly developed while the entoconid-posterolophid ridge is not so strong and shows no signs of extra cusps taking part in the formation of the posterolophid; in *Sciuropterus* the reverse condition is observed. Finally, in *Pliosciuropterus* and *Petauria* there is little, or no, development of the trigonid basin, having the metalophids either absent or reduced to short, low lophids which fade off into the talonid basins.

*Sciuropterus grimmi*, itself, is probably descended from *Sciuropterus albanensis*. It differs from that species in being considerably larger (Table 1), in having a more well defined trigonid basin with stronger metalophids, in reduced rugosity of the talonid, and in possessing somewhat shallower buccal valleys around the mesoconid.

Table 1  
Measurement of species of *Sciuropterus*

	alveolar diastema length length									
	P <sub>4</sub> -M <sub>3</sub>		P <sub>4</sub> a-p tr.		M <sub>1</sub> a-p tr.		M <sub>2</sub> a-p tr.		M <sub>3</sub> a-p tr.	

*S. gaudryi*

Lyon # 87	8.1	4.0	1.7,	1.4-1.7	1.8,	1.9-2.1	—	—	—	—
Lyon # 88	8.4	—	1.8,	—	1.8,	1.9-2.1	2.0,	2.3-2.3	2.4,	2.4
Lyon # 89	—	—	—	—	1.9,	1.9-2.1	2.1,	2.3-2.3	2.3,	2.1

*S. albanensis*

Type BMNH #										
M 5286	13.8	6.5	3.0,	2.5-2.9	3.1,	3.1-3.3	3.4,	3.4-3.4	4.0,	3.4-3.0
Lyon # 85	13.2	6.5	2.7,	2.3-2.8	3.0,	2.9-3.2	3.2,	3.3-3.3	3.4,	3.3-2.8
Lyon # 91	14.2	6.8	3.2,	2.4-2.8	3.1,	3.0-3.2	3.3,	3.3-3.3	4.0,	3.2-2.8
Lyon # 290	14.5	6.3	—	—	3.2,	2.6-3.2	3.5,	3.2-3.6	4.1,	3.5-3.5
Type of <i>S. jourdani</i>										

*S. lappi*

(MEIN 1958)	14.5-15*)	—	3.3,	3.0	3.1,	3.3	3.7,	3.6	4.5,	3.7
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*S. grimmi*

München 1952 X 80	15-16*)	—	—	—	3.7,	3.2-3.8	4.0,	3.6-3.9	4.3,	3.8-3.6
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*Pliosciuropterus dehnli*

(SULIMSKI 1964)	10.5-11.1	—	—	—						
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*Petauria helleri*

(DEHM 1962)	16.2									
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\*) estimated from analogy with other species for length of P<sub>4</sub> in relation to M<sub>1</sub>-M<sub>2</sub>

Sciurus sp.  
Plate 6, fig. A—B

**Material:** Munich 1952 X 127, part of palate with infraorbital foramen, LP<sup>1</sup>, LM<sup>2</sup>, and RM<sup>2</sup>.

**Description:** This fragment is badly broken but the area around the infraorbital foramen is preserved and shows that the foramen is triangular in cross section with a long infraorbital canal. It is not compressed into a narrow vertical slit as it is in *Sciurus* but more closely resembles the condition seen in *Citellus*. The masseteric tubercle is small and lies just below the infraorbital foramen.

The upper dentition is *Sciurus*-like and bears no resemblance to that of the *Citellus* group of sciurids. The P<sup>1</sup> is large with a wider anterior cingulum and high parastyle. The protocone lies opposite the paracone and is moderately expanded anteroposteriorly. The metaloph passes obliquely across the tooth and a distinct metaconule is present. Internally the posterior cingulum is wide but it narrows to a thin shelf at the postero-buccal margin. Both the protoloph and metaloph are low.

The second molars are broad and low crowned. The anterior cingulum is quite wide with little parastylar development. The protoloph and metaloph are very low and show no trace of conules. These lophs drop steeply from the tops of the paracone and metacone and fade into the internal face of the protocone. No mesostyles are present.

Measurements in mm.

	a—p	tr.
LP <sup>1</sup>	1.6	1.7
LM <sup>2</sup>	1.6	1.9
RM <sup>2</sup>	1.6	1.9

**A f f i n i t i e s:** The dentition indicates that this specimen represents a small species of *Sciurus* as it presents the typical tree squirrel condition of simple crown pattern, broad protocones and low lophs. This form differs from the Vindobonian *Sciurus bredai* in having a much larger P<sup>1</sup> in relation to M<sup>2</sup> than does *S. bredai* and also the lophs are much lower in the Markt species than in *S. bredai*. In both these respects *Sciurus* sp. is more typical for tree squirrels than is *S. bredai* and there is considerable question as to whether *S. bredai* really represents *Sciurus* in its true sense. This question will be considered in detail in a later paper.

One character, the rather open, oval infraorbital foramen, argues against placing this specimen in *Sciurus*, however. In Recent *Sciurus* the infraorbital foramen is greatly compressed into a narrow dorso-ventrally elongate slit and it is generally situated well forward of the tooth row. In the present specimen the foramen lies just anterior to the alveolus of P<sup>3</sup> and it is not compressed. None of the zygomatic plate is preserved in the present specimen, making it impossible to



determine the extent of masseter migration on the rostrum, which is the factor controlling compression of the infraorbital foramen, although the condition of the foramen suggests that the masseter had not expanded anteriorly to any great extent. As the dentition is so typically that of *Sciurus*, this specimen is best referred to that genus until more material is known.

### Specimens incorrectly referred to the Sciuridae

„*Sciurus*“ *chalaniati*

Plate 4, fig. F

FREUDENBERG (1941, p. 116) referred five specimens from Gaimersheim to *Sciurus chalaniati* (POMEL). Much of this material has been lost but there is one jaw remaining in the collections from this sample. This single specimen (see Freudenberg, 1941, pl. 13, fig. 18) is clearly related to *Gliravus*.

In the original description of *Sciurus chalaniati*, POMEL (1853) neither figured a specimen of this species nor gave any statement of its characteristics. FILHOL (1879, pl. 3) figured specimens which he referred to *Sciurus chalaniati* but added little in the way of a description of the species, saying only that “la forme des dents est exactement la même que celle du *Sciurus feignouxii*”, and that *S. chalaniati* was smaller than *S. feignouxii*. None of FILHOL's nor POMEL's material of *S. chalaniati* was found by me in the Paris collections in 1964 and to my knowledge there are no specimens extant which can be unequivocally referred to POMEL's species. The specimens figured by STEHLIN & SCHAUB (1951, p. 16, fig. 11) as *Sciurus chalaniati* are not *S. chalaniati* but *Sciurus costatus* (FREUDENBERG, 1941). As there has never been any adequate basis for an understanding of what *S. chalaniati* is, it is only compounding nomenclatorial confusion to refer new material to this species, at least until such a time as some of the original specimens on which the name was based are found, described and figured. The specimens from Coderet referred to *Sciurus* aff. *chalaniati* by VIRET (1929, p. 58) were so assigned purely on the basis of size and it has been shown recently (HUGUENEX, pers. communication) that the Coderet specimens are identical to some from Gaimersheim which were described by FREUDENBERG (1941) as *Sciurus costatus*.

Following FREUDENBERG and undoubtedly using the glirid jaw mentioned above for comparison, SCHALK (1957, p. 73 and fig. 8) assigned a single tooth from Burgmagerbein to *Sciurus chalaniati*. This molar is also that of a glirid, in this case possibly of *Dryomys*.

„*Sciurus*“ *schlosseri* FREUDENBERG

Type. Munich 1951 I 175, left mandible with P<sub>4</sub>—M<sub>3</sub>.

In his paper on the Gaimersheim rodents FREUDENBERG included the description of new species from other localities. One of these was *Sciurus schlosseri* based on a jaw from the Phosphorites de Quercy. The dentition of this specimen

(FREUDENBERG, 1941, pl. 13, fig. 1) is badly worn but enough of the crown pattern remains to show clearly that the specimen is a pseudosciurid, not a sciurid. The molar cusps have an alternating alignment, the anterior cingulum passes internally completely along the anterior face of the metaconid, and a strong hypolophid is present on  $P_4-M_3$ . These characters all serve to distinguish *Adelomys* from any sciurid and this specimen clearly belongs in that genus. It is probably a specimen of *Adelomys quercyi* SCHLOSSER.

*Paracitellus eminens* DEHM

Plate 4, fig. E

Type. Munich 1937 II 10102, right mandible with  $P_4-M_2$ .

DEHM (1950, p. 331) described a new rodent from the Burdigalian Wintershof-West fauna as *Paracitellus eminens* and referred this species to the Sciuridae. In his discussion (op. cit., p. 357) he pointed out certain resemblances of *Paracitellus eminens* to *Plesispermophilus* of the Phosphorites de Quercy including similarities in tooth proportions and in the height of the metaconid. When comparing *Paracitellus* with Pliocene and Pleistocene ground squirrels DEHM noted the following differences between the two: termination of the incisor under  $M_2$  rather than under  $M_3$ ; the anterior zygomatic root lying opposite  $P^4$  rather than just anterior to  $M^1$ ; and fewer roots on the premolars of *Paracitellus* than on those of *Citellus*.

In making comparisons between *Paracitellus* and other Tertiary rodents DEHM overlooked a number of characters which argue against sciurid affinities for this genus. As he pointed out, the anterior zygomatic root lies far forward, but Munich 1937 II 10112 also shows that the inferior border of the zygoma bears a small muscle scar for the masseter and that the infraorbital foramen is round with no masseteric tubercle present. There is no indication of even partial development of a zygomatic plate. The condition of the infraorbital foramen and zygomatic arch is identical to that seen in Munich 1937 II 10101, a specimen of *Ameniscomys* and is indeed typical for a protrogomorph rodent. The absence of any sciuriform masseteric complex in *Paracitellus* is also borne out by the structure of the mandible and masseteric fossa. There is no distinctly concave masseteric fossa, but rather only an acutely triangular plate which terminates under the posterior border of  $M_2$ . The ascending ramus and area for insertion of the masseter is also protrogomorph rather than sciuriform.

In the dentition there are many characters that remove *Paracitellus* from any relationship to the Sciuridae. The absence of both protoloph and metaloph and the sharply triangular primary cusps and conules in the upper molars distinguish *Paracitellus* from all sciurids, as do the deep notch down the anterior face of  $P_4$ , the large open trigonid basins of  $M_1-M_2$ , and the extremely elongate condition of  $P_4-M_2$ . The incisor is not laterally compressed as it is in all sciurids.

As DEHM showed there are many differences between *Paracitellus* and *Plesispermophilus* and there is also a considerable lapse of time between the two occur-

rences. The lower dentition of *Plesispermophilus* (STEHLIN & SCHAUB, 1951, fig. 468—470) has many characters in common with *Paracitellus* including the notch down the anterior face of  $P_4$ , the generally elongate shape of  $P_4$ — $M_2$  and the wide, open trigonid basin. There are certain accessory lophs in the talonid basins in *Plesispermophilus* not seen in *Paracitellus* but faint remnants of these lophs do appear in the Burdigalian form. Reduction and loss of these structures could easily have occurred between the early Stampian and the Burdigalian. In the structure of the mandible and infraorbital area *Paracitellus* is certainly protogomorph and thus much closer to *Plesispermophilus* and the Paramyidae than to any member of the Sciuridae.

*Paracitellus eminens* should be transferred to the family Paramyidae, subfamily Prosciurinae. It shows no special relationship to the Sciuridae.

DEHM (op. cit., p. 359 and 367) also described additional material of *Paracitellus* as *Paracitellus*, n. sp. A and B. The mandible assigned to *Paracitellus*, n. sp. A (op. cit., fig. 34 a—b) and the two mandibles described as *Paracitellus*, n. sp. B are also clearly protogomorph and are paramyid, not sciurid. The other material assigned to *Paracitellus*, n. sp. A is sciurid, however, and represents a new species of *Sciuropterus*. This was first suggested by JAMES (1963, p. 87—88) and examination of this material has left no doubt that it represents *Sciuropterus*, although the few isolated teeth known to date are insufficient to characterize this species. The upper molars have complete protolophs and metalophs, small accessory lophs from them, and rather indistinct conules. The lower molars are wider than long, and have small trigonid basins and rugose talonid basins. These characters are quite in contrast to those seen in *Paracitellus*. This is the earliest record for *Sciuropterus*.

MEIN (1958, p. 67—68) refers several specimens from Vieux-Collonges to “*Paracitellus eminens*?” and to “sciurid indet. size of *Paracitellus* A.” These specimens are referable to *Sciuropterus* and are probably only variants of *Sciuropterus lappi*.

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Plate 4. Figures A and B, *Sciuropterus* cf. *S. gaudryi*, 1952 XIV 20, RP<sup>4</sup> and 1952 XIV 293, RM<sup>1</sup> or <sup>2</sup>, X 10. C and D, Sciurid incertae sedis, 1952 XIV 21, LP<sub>4</sub>-M<sub>1</sub> and 1952 XIV 288, LM<sub>1</sub> or <sub>2</sub>, X 20. E, Type *Paracitellus emineus*, 1937 II 10102, RP<sub>4</sub>-M<sub>2</sub>, X 5. F, *Sciurus cbalaniati*, 1952 II 185, LP<sub>4</sub>-M<sub>2</sub>, X 10.

Plate 5. Figures A and B, *Sciurus* sp., 1952 X 127, LP<sup>4</sup> and LM<sup>2</sup>, X 20. C, *Sciuropterus* cf. *S. gaudryi*, 1952 XIV 20, RP<sup>4</sup>, X 20. D, *Sciuropterus* sp., 1952 X 83, LM<sup>1</sup> or <sup>2</sup>, X 20. E, Sciurid incertae sedis, 1952 XIV 21, LP<sub>4</sub>-M<sub>1</sub>, X 20.

Plate 6. Figures A and B, *Sciurus* sp., 1952 X 127, LP<sup>4</sup> and M<sup>2</sup>, and RM<sup>2</sup>, X 10. C, *Sciuropterus* sp., 1952 X 83, LM<sup>1</sup> or <sup>2</sup>, X 10. D, *Sciuropterus grimmi*, n. sp., Type, 1952 X 80, LM<sub>1</sub>-M<sub>3</sub>, X 10.



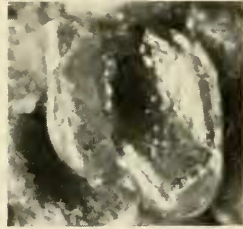
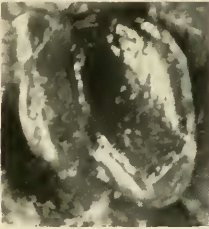
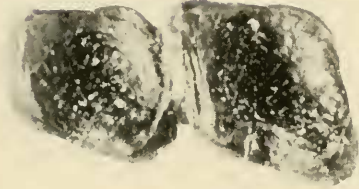
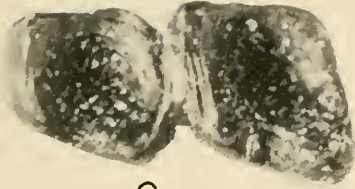
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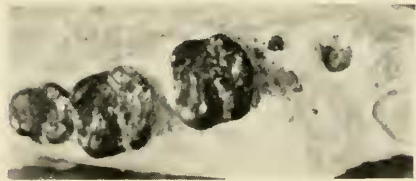
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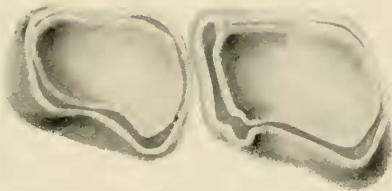
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